Foraging habitat and performances of King penguins *Aptenodytes patagonicus* Miller, 1778 at Kerguelen islands in relation to climatic variability

by

Charles-André BOST* (1), Anne GOARANT (2), Annette SCHEFFER (1), Philippe KOUBBI (2), Guy DUHAMEL (3) & Jean-Benoît CHARRASSIN (3)

ABSTRACT. - Understanding how climate change affects the foraging ecology of key marine predators is an important issue in the study of Southern Ocean food webs. Since 1998, we have conducted a long term research program on the foraging ecology of a top-diving predator, the King penguin *Aptenodytes patagonicus*, simultaneously at Kerguelen and Crozet Islands with the support of the IPEV (Institut Polaire Français). King penguin is one of the most important predatory birds at Kerguelen. In summer, they forage preferentially along large-scale physical features and use the three dimensions of hydrographic features to feed on myctophid fishes (the penguins' main prey and a major prey species in the Southern Ocean). Primarily, this study aims to evaluate how the change in foraging parameters and success of penguins reflect the impact of oceanographic conditions on key food webs in the polar frontal zone. Each summer, breeding (incubation and brooding) penguins from the Ratmanoff colony (Courbet Peninsula, Kerguelen; 100000 pairs) are instrumented with Argos transmitters or GPS with time-temperature-depth recorders. Here we provide a first modelling approach to the King penguin's foraging habitat during summer from static variables (bathymetry), dynamic variables (SSHt, SST, Chlorophyll) and their related trends (gradients). In addition, trawl data on the distribution of myctophid fishes have been integrated. The most important factors explaining penguin foraging location are the SSHt, the bathymetry gradient and the SST. Results of interannual change in penguins at-sea trajectories, diving behaviour, foraging success and effort are discussed according to the interannual changes in the hydrographic structure in the Kerguelen region.

RÉSUMÉ. - Habitat d'alimentation du manchot royal (*Aptenodytes patagonicus*) à Kerguelen.

Comprendre comment les changements climatiques vont affecter les prédateurs supérieurs marins de l'océan Austral et les chaînes trophiques dont ils dépendent est d'un intérêt majeur. Depuis 1998, nous menons un programme de recherche à long terme sur les stratégies alimentaires d'un prédateur marin plongeur, le manchot royal *Aptenodytes patagonicus* aux îles Kerguelen et Crozet, avec le support de l'IPEV (Institut Polaire Français). Le manchot royal est un des prédateurs marins les plus importants de Kerguelen, en termes de biomasse consommante. En été, les manchots royaux se nourrissent préférentiellement de poissons de la famille des myctophidés, un groupe clé des chaînes trophiques de l'océan Austral. Ils recherchent leurs proies préférentiellement au niveau de caractéristiques physiques à grande échelle et utilisent les 3 dimensions de la structure hydrologique. Un des objectifs de notre étude est d'évaluer comment les changements dans l'écologie alimentaire des manchots vont refléter l'impact des conditions océanographiques à l'échelle locale et à grande échelle, sur les chaînes alimentaires dont ils dépendent. A cette fin, des manchots partant en mer pour se nourrir sont équipés de balises Argos, GPS ou enregistreurs de plongée / température de l'eau, durant chaque été austral. A Kerguelen, la colonie étudiée est située à Ratmanofff, sur la façade est de la péninsule Courbet (100000 couples). Nous présentons ici la première approche de modélisation de l'habitat alimentaire en mer des manchots, à partir de l'analyse des variables statiques (bathymétrie) et dynamiques (température et hauteur de l'eau et leurs gradients, chlorophylle et gradients associés). Les données des pêches scientifiques existantes sur la distribution des myctophidés ont été intégrées. Les facteurs explicatifs les plus importants vis-à -vis de la distribution en mer des manchots sont les anomalies des hauteurs d'eau et les gradients associés, la température de l'eau et le gradient de bathymétrie. Les résultats des changements d'année en année des trajectoires en mer des manchots, du comportement de plongée et de leur effort de pêche sont discutés en perspectives des changements hydrologiques affectant l'écosystème de Kerguelen.

Key words. - Climate variability - Top-predators - Penguins - Foraging - Habitat modelling - Kerguelen.

The Southern Ocean is one of the marine areas most susceptible to climate change (Trathan *et al*., 2007). The detection and quantification of the impact of the climatic variability on the biodiversity of this ocean and its food webs have been given high international priority because it still accommodates the planet's largest unexploited animal bio-

(1) Centre d'Études biologiques de Chizé, CEBC-CNRS, 79360 Villiers-en-Bois, France. [annette.scheffer@gmx.de]
(2) Laboratoire d'Océanographie de Villefranche, Station zoologique-La Darse, BP 28, 06230 Villefranche, France. [anne.goarant@wanadoo.fr [koubbi@univ-littoral.fr]
(3) Département Milieux et Peuplements aquatiques, UMR 5178, USM 401, 43 rue Cuvier, CP 26, 75231 Paris CEDEX 05, France. [duhamel@mnhn.fr] [jbc@mnhn.fr]
* Corresponding author [bost@cebc.cnrs.fr]

mass (Atkinson *et al.*, 2004). However, the links between the physical features of the Southern Ocean, biological productivity and the distribution and abundance of zooplanktonic and nektonic prey remain poorly understood.

Considering these difficulties, it has been proposed that the foraging behaviour of tagged predators could be used as bio-indicators of the availability of underlying resource distribution (Wilson *et al.*, 1994; Bost *et al.*, 1997; Wilson *et al.*, 2002; Austin *et al.*, 2006). Many marine birds from these areas are wide-ranging predators, highly mobile, and dependent on secondary and tertiary productivities. At sea, they strive to forage efficiently to maximize their chances of reproductive success (Lescroël *et al.*, 2010).

Most research efforts concerning pelagic resources in the Southern Oceans have been devoted to the change in the status of krill stocks (Atkinson *et al.*, 2004). However, the mesopelagic fishes (Family Myctophidae) are also an important biological resource, in which biomass is estimated at 200-400 x 10^6 tons (e.g., Lubimova *et al.*, 1987; Pakhomov *et al.*, 1994). Additionally the distribution of these small schooling fish is closely related to the thermal structure of the water mass (Torres and Somero, 1988). Myctophids are difficult to sample using traditional techniques because of their patchy distribution and mobility (Duhamel 1998). Diving top predators such as King penguins *Aptenodytes patagonicus* Miller 1778 are good candidates to investigate the inter-annual and long-term change in myctophid distribution. King penguins are one of the most important avian consumers of the Southern Ocean (Guinet *et al.*, 1996). It is also one of the most specialized seabirds in terms of diet, relying almost exclusively on myctophid fishes during the summer (Cherel and Ridoux, 1992). They are deep divers and pelagic foragers able to routinely dive deeper than 250 m and to forage up to 400 km from their colonies (Bost *et al.*, 2002).

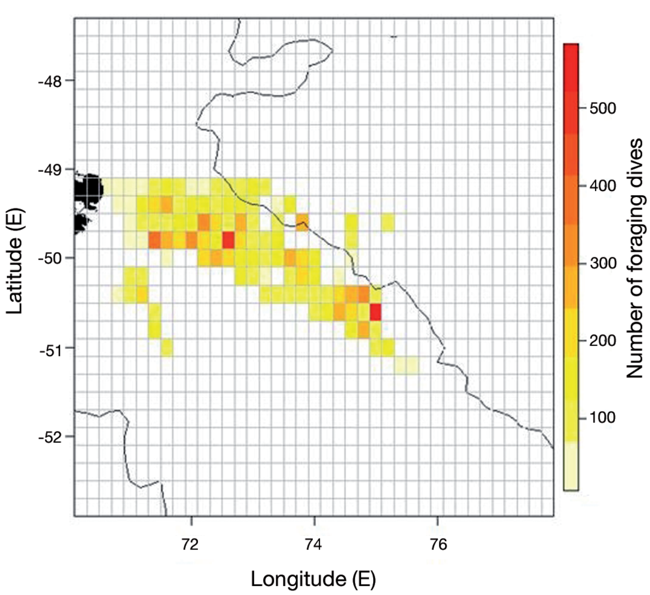

Figure 1. - Foraging dives distribution of King penguins satellite-tracked from Ratmanoff Colony, East of Kerguelen Islands (n = 4 years, 1998-2002, 27 271 dives, n = 27 birds).

Since 1998, we have conducted a long term research program on the King penguin foraging ecology at Kerguelen Islands. The aim of the project is to evaluate how the changes in foraging parameters and success of an avian top predator can reflect and predict change in the availability of myctophids in one of the most productive ecosystem of the Polar Frontal Zone, the Kerguelen archipelago.

Here we provide a first modelling approach of the King penguins foraging habitat during summer at Kerguelen. The habitat model was developed to explain and predict spatial distribution of foraging effort within the penguins' available geographic range. This was carried out from the analysis of penguins foraging activity (*via* a bio-logging approach) over four years (1999-2002) concurrently with both datasets describing physical and biological oceanography.

MATERIALS AND METHODS

The project relied on the long-term monitoring of penguins movements at sea and foraging effort during the breeding season depending on oceanographic conditions. Each summer, breeding (incubation and brooding) penguins from the Ratmanoff colony (Courbet Peninsula, 100 000 pairs) are instrumented with Argos transmitters or Fast-loc GPS (Sirtrack: Havelock North, NZ), and Time-Temperature-Depth recorders (MK7 to MK9, Wildlife Computers: Redmond, WA, USA).

We used the spatial distribution of dives to determine the at-sea distribution of the foraging habitat. Only dives deeper than 50 m were used as most of the feeding activity occurs beyond that depth (Charrassin *et al.*, 2002a). This corresponded to a total of 27 271 foraging dives recorded on 27 birds from 1998 to 2002. A grid of 0.2° cell size was designed over the Kerguelen shelf and in each cell the number of dive was recorded. Only cells where at least three different individuals had dived were kept (n = 107, 54% of the dives; Fig. 1). The number of foraging dives was then log-transformed. Finally the number of dives per grid cell was modelled according to three types of environmental components: the spatial, physical and biological component. Dynamic oceanographic variables (surface height, sea surface temperature, chlorophyll concentration) were extracted for each grid cell from both sources of oceanographic information (model and satellite), whereas static variables such as bathymetry was obtained from the National Oceanic and Atmospheric Administration's (NOAA) ETOPO dataset, and their gradient (in terms of slope between each cell) computed.

In addition, myctophid presence-absence (distribution trawls data on the Kerguelen shelf from the *Ichtyoker* data-

base, 1998-2000) was modelled according to the four previous environmental variables and their gradient. A model was performed using Random Forests, a machine-learning method combining three models trained on different bootstrap replicate sample of the data (Elith and Graham, 2009). We used data from night trawls at depths ranging from the surface to 100 m (n=73 trawls), performed from January to March (Duhamel 1998; Guinet *et al*., 2001). The performance and evaluation of the model was evaluated using a Leave-one-out cross-validation.

The variable testing procedure for assessing penguin foraging habitat was based on the test of the main variables and their possible combinations, which provided seven hypotheses (Tab. I). A bootstrap procedure (Potts and Elith, 2006) was performed to evaluate the performance of each modelling hypothesis (10 000 simulations).

Table I. - Tests of the hypothesis predicting the distribution of the king penguin foraging habitat at Kerguelen Islands (RMSE: Root Means Square Error; AVE: Average Error). The letters m and b correspond to the coefficients of a linear regression between the observed and predicted values: observed = m × predicted + b. The hypothesis with the best performance is indicated in bold.

Hypothesis	Pearson	Spearman	m	b	RMSE	AVE	Variance explained
“Space”	0.652	0.631	1.232	-0.467	0.259	0.000	27.9%
“Physical Environment”	0.667	0.487	1.502	0.025	0.236	0.004	28.1%
“Prey”	0.481	0.142	1.017	-1.326	0.278	-0.001	17.3%
“Space + Environment”	**0.787**	**0.703**	**1.217**	**-0.448**	**0.203**	**0.004**	**45.1%**
“Space + Prey”	0.741	0.647	1.311	-0.635	0.222	0.001	39.3%
“Environment + Prey”	0.665	0.487	1.515	-0.044	0.238	0.006	29.1%
“Space + environment + prey”	0.784	0.690	1.251	-0.518	0.203	0.004	43.7%

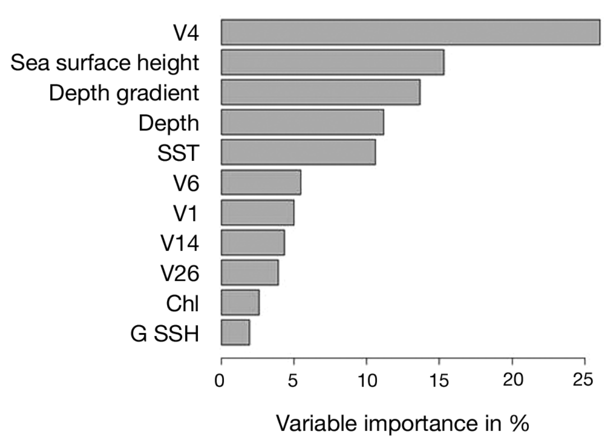

Figure 2. - Output of the foraging habitat model showing the most important variables (Hypothesis “Space + environment”). V1: large scale distribution of dives (Kerguelen North and South); V4: mesoscale distribution of dives (range 100 km, including the 2 areas of highest diving activity); V6: mesoscale distribution of dives (range 76 km, limit of the studied area); V14: mesoscale distribution of dives (range 52 km, restricted diving zones, Kerguelen North); V26: mesoscale distribution of dives (range 47 km); V34: fine scale distribution of dives (range < 10 km) [not shown].

RESULTS AND DISCUSSION

At Kerguelen, King penguins are distributed in an area dominated by complex interactions between the proximity of the polar front, bathymetry and current advection. They forage at a mean distance of 300 km off the colony and target mainly waters along the shelf break that are associated with the Polar Front. We used the most important physical and biological variables and parameters likely to determine the penguin’s foraging distribution.

The three main influencing variables follow. First, the spatial distribution of dives, which are strongly autocorrelated at different scales. To determine the corresponding spatial scales, a principal coordinate analysis of neighbour matrices (PCNM) was performed (Dray *et al*., 2006) (Tab. I). Six spatial scales were retained in the analysis (Fig. 2). Second, the environmental variables, which includes the physical (static: bathymetry; dynamic: SST, sea surface height anomaly) and biological variables (chlorophyll). Lastly, the prey fields (myctophids) obtained from the model.

Overall, the hypothesis combining spatial and environmental variables had the best average performance (45% of explained variance, Tab. I). The output of the foraging habitat model indicated the contribution of the most significant variables (Fig. 2), primarily, the variable combining the spatial distribution of dives and environmental variables; and secondly, two significant dynamic variables, sea surface height and sea surface temperature. Static variables, like depth gradient and depth, also play a significant role.

Intrinsically, modelling of the King penguin’s foraging habitat based on a four-year study of diving activity indicates the importance of physical variables such as the temperature of the water mass and sea surface height. Other studies have shown how oceanic foragers such as King penguins concentrate their foraging effort in colder waters of the Polar Frontal Zone where myctophids tend to aggregate (Cotté *et al*., 2007; Bost *et al*., 1997). In the Crozet sector, the foraging activity occurs within mesoscale frontal zones and strong currents, both associated with eddies at the Polar Front (Cotté

et al., 2007). However, this study also confirms the role of the extensive Kerguelen plateau as a major physical variable driving the foraging behaviour of such pelagic forager (Charrassin *et al*., 2002b). Climate change scenario predicts a major southern shift of the polar front during this century (Solomon *et al*., 2007). In the future, warmer surface waters and increased frequency of mesoscale warm anomalies may alter the myctophid distribution and the foraging success of the penguins and other top-diving predators. Next steps will be to model the foraging habitat/prey distribution in distinct climatic scenarios and to evaluate the foraging responses of the penguins in different modelled foraging habitats by using Behaviour Based Models (Grimm and Railsback, 2005).

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